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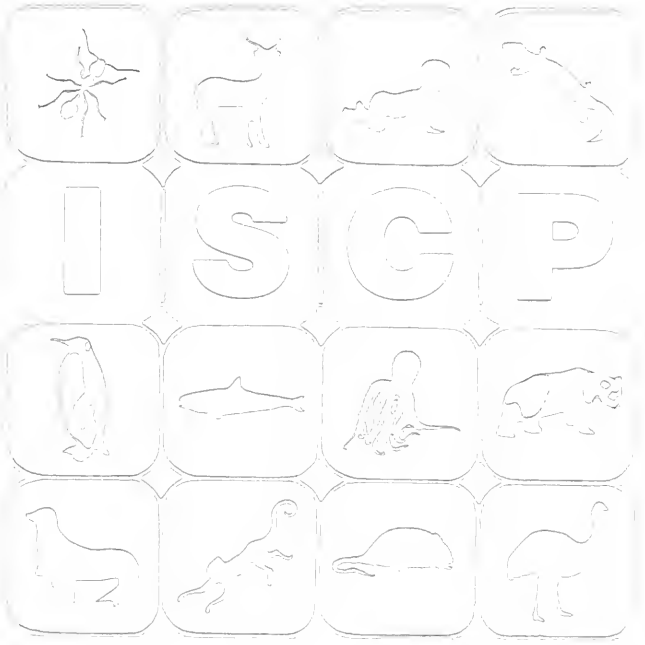

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NUMERICAL COMPETENCE IN FERRETS (*Mustela putorius furo*)

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University of Guelph

ABSTRACT: Ferrets were tested in a free feeding situation that required them to eat only three pieces of food from a randomly sized larger array containing between 15 - 20 items. Controls were established to preclude discrimination based on spatial or volumetric cues, or cuing by the experimenter. This demonstration represents the first evidence of numerical competence in a mustelid species, and replicates the results of pioneering research by Koehler and his associates with budgerigars (Marold, 1939), as well as more recent work with rats (Davis & Bradford, 1991). Although the performance of ferrets reached comparable levels to those reported with other species, extended training yielded a deterioration in performance. These results are discussed in terms of the role of consequences to suppress competing responses, a problem that has been reported to underlie a variety of learning situations with ferrets.

Various forms of numerical competence have been demonstrated in a host of mammalian and avian species (e.g., Boysen & Berntson, 1989; Davis, 1984; Davis, MacKenzie & Morrison, 1989; Koehler, 1950; Pastore, 1961; Pepperberg, 1987). Indeed, following a half century of research, it is no longer reasonable to treat numerical ability as a distinctly human domain (Davis & Perusse, 1988a; Honigmann, 1942).

Despite a substantial body of literature and a burgeoning research agenda (e.g. Boysen & Capaldi, 1993), there has been no attempt to demonstrate any form of numerical competence in a mustelid species. This lack of attention to mustelid learning is not altogether general. Mustelids have been tested for other forms of cognitive competence with mixed results. In 1950, Beach reported that efforts at food-rewarded maze learning in ferrets were largely unsuccessful. He observed that ferrets, unlike more conventional psychological subjects, continued to explore blind alleys.

The general impression that ferrets were a "headstrong" species was

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maintained by Pollard & Lewis (1969). Although these authors reported some degree of success in training ferrets to navigate a maze successfully, Pollard & Lewis reported that "Unless food can be obtained rapidly...large numbers of competing responses are to be expected from this species." (1969, pg 42). In contrast to these reports, Haddad, Rabe, Dumas & Lazar (1976) described ferrets as a "readily trainable animal," although they observed that this species continued to be an uncommon subject in behavioral studies.

The situation has not changed much in the ensuing 20 years, either with regard to mustelid learning studies in general, or numerical competence in particular. Arguably, mammalian species that share an econiche might undergo similar selection pressure to develop cognitive abilities. Although much is known about the rodent's numerical competence (e.g. Capaldi & Miller, 1988; Davis & Bradford, 1986; Koehler, 1950), the related capacities of its frequent mustelid predator remain untested.

The present study examines for the first time the ability of the common ferret, *Mustela putorius furo*, to discriminate the quantity three and use this information in a simulated foraging situation. The technique we have selected derives from pioneering work by Otto Koehler (1950) and his associates. In their original demonstration (Marold, 1939), budgerigars were trained to eat a fixed number of food items from a larger array of freely available food. More recently, Davis & Bradford (1991) successfully employed this technique with rats, marking the first time that absolute numerical cues were used to restrict foraging behavior in a mammal. The present experiment attempts to replicate this form of numerical competence with ferrets.

METHOD

Subjects

Two albino ferrets (*Mustela putorius furo*), one male and one female, served as subjects. Both animals were obtained at approximately eight months of age from a veterinary clinic which received them from a family unable to care for them. Both animals were spayed prior to experimental testing.

Subjects were housed individually, but were allowed a "social time" for approximately two hours per day. During this period, subjects were permitted to interact freely in a 10 x 12 foot room that contained cloth bedding material, plastic tunnels for shelter and various toys. Food

rations (Hills Science Diet, Feline Maintenance 200 mg pellets) were provided to maintain approximately 95% of free feeding body weights for the duration of the experiment. Water was continuously available.

Apparatus

The experimental apparatus (illustrated in Figure 1) included a start area and test surface. The start area consisted of the seat of an upholstered chair (approximate surface 0.4 x 0.4 m). The test surface was a Melamine coated plank, approximately 0.6 m wide, which extended 2.4 m from below the edge of the start area. To prevent food pellets from being lost, 2 cm high sides were added to the edges of the test surface. A removable wooden barrier 0.6 m wide and 0.5 m high was placed on the plank next to the start area to prevent the subject from viewing the test surface or leaving the start area before the experimenter was ready to begin a trial.

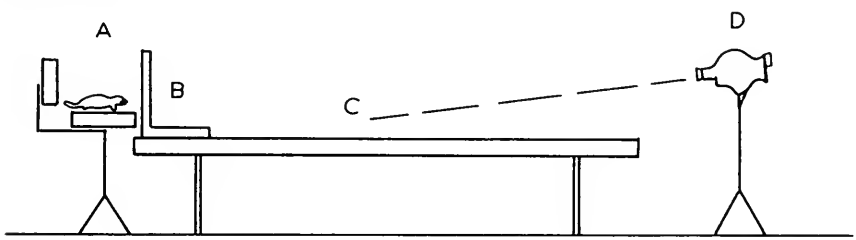

Figure 1. Representation of experimental apparatus showing location of (A) start area with subject, (B) wooden barrier, (C) test surface where food items were displayed, and (D) video recorder.

Procedure

Experimental sessions were performed once a day during each of the following stages.

Habituation. During the initial week, subjects were handled for approximately 20 minutes per day, not only to provide "gentling", but also to encourage a bond that would facilitate the use of social reinforcement during testing (Davis & Balfour, 1992; Davis & Perusse, 1988b). Handling was continued during a second week, during which food pellets (8 in 1 Ferret Diet, Pet Products Inc., Hauppauge, NY) were fed by hand. Hand-fed pellets would later be used as partial reward for successful completion of a trial. During the third week, animals were introduced to the experimental apparatus and shaped to eat several pellets off the plank, as well as from the experimenter. By the end of the

third week, subjects had learned to start a trial by jumping down approximately 10 cm from the start area of the chair (A in Figure 1) to the plank (C in Figure 1). Subjects were permitted to explore the test surface, and were rewarded with both food items and social reinforcement (petting and vocal praise) for returning to the start area after consuming food from the plank.

Training. A total of 12 training sessions were conducted. Subjects were shaped to eat exactly three pellets, their "target number," from a larger array of food on the plank. 8 in 1 Ferret Diet, a non-precision milled pellet, was specifically used in order to control for volumetric cues. These food items vary considerably in both shape and weight. A randomly drawn sample of 30 pellets used during training and testing averaged 210 mg in weight (range = 130 - 286 mg; standard deviation = 46.1 mg). Thus, it required nearly seven food items of the smallest kind to match the volume of three large ones.

Initially the array of food consisted of exactly the target number of pellets. Gradually, between one and five additional pellets were added. Initially, these additional pellets were spatially separated from the target number by between 0.1 and 0.5 m. This separation was gradually reduced to zero over the course of training. The number of pellets in the array was also increased to between 15 and 20. Array patterns were varied randomly to prevent performance based upon pattern recognition.

Five trials were run during each session. A correct trial consisted of the subject consuming its target number of pellets and returning to the start area without consuming any of the remaining pellets. Correct trials were scored as soon as the animal turned its body and began to return to the start area. Verbal praise was delivered as the animal moved back to the start area. Upon climbing up to the surface of the chair, the subject was further rewarded with petting and praise, as well as one or two extra food pellets fed by hand.

An incorrect response consisted of consuming either less or more than the target number. An error trial involving too few pellets being eaten resulted in neither positive nor negative reinforcement being delivered when the subject returned to the start area. The trial was simply recorded as an error. Attempts to consume more than the target number were immediately followed by a handclap, foot stomping and yelling the word "no!". Such negative consequences were delivered as soon as the subject made physical contact (either by paw or mouth) with a fourth piece of food. This typically caused the subject to drop the pellet and return to the start area. This form of aversive control was occasionally insufficient to control behavior of the male subject, and so it was occassionally supplemented by a light slap on the nose or posterior.

In the majority of cases, errors designated "More than" involved only a fourth pellet being consumed. Approximately 10% of such errors involved contact with a fifth pellet before consequences were effective in suppressing behavior.

Testing. Data collection was begun during this Phase. Four trials were run during each session. Correct responses and errors were recorded and continued to be rewarded with food and social contact and/or negative consequences following completion of a trial. In order to minimize the amount of feedback during testing, praise was no longer delivered during a trial as it had been during the training phase. Following each trial, regardless of its outcome, the animal was required to return to the start area in order to "reset the counter to zero" and signal the end of a trial.

The temporal spacing of trials was determined by both the subject and experimenter. A sequence of four correct trials could proceed without intervention by the experimenter. Following an incorrect trial, however, a Time Out (range 10 - 30 sec) was imposed. The experimenter intervened by inserting the barrier (B in Figure 1) and replenishing the food array as required. The next trial began when the barrier was removed.

Pellet arrays were located between 0.5 and 1.0 m from the start area and consisted of between 15-20 food items on the initial trial of each session. Pellets were located approximately 3 cm apart on the average, with interpellet space ranging between 8 mm and 5 cm. Because the animal progressively reduced the number of pellets remaining on each trial, it was occasionally necessary to replenish the plank between trials in a session. No systematic criteria were used for when pellets were replenished between trials, or for the number of pellets added to the array. This non-systematic approach was chosen to provide greater variability in the size of arrays confronted by the animals across both trials and sessions.

Small Pellet Control Procedure. Two control sessions were run during which broken pellets and small pieces of food were used exclusively. These sessions occurred during the final block of 80 trials illustrated in Figure 2. A sample of food items drawn from the same source as those used during "small item" probe trials revealed that their average weight (80.9 mg; range 40 - 133 mg; standard deviation = 23.9) was less than 40% of normally sized pellets. All other aspects of the test procedure were identical during these two control sessions.

The experimenter remained situated behind the start area in back of the subject during all sessions. Thus, animals moved in a direction away from the experimenter as they foraged on the plank. Test sessions were

run for approximately 480 trials, followed by a series of control sessions for the "Clever Hans" effect.

Clever Hans Control Procedure. In order to determine whether numerical discrimination depended on the presence of subtle cuing from the experimenter, four sessions were conducted during which the experimenter was removed from the room during testing. No feedback was given, regardless of performance, during these sessions. A sufficient supply of food items was provided so that four consecutive trials could be run without replenishing the array on the plank. A video tape record was made of each session for analysis. Clever Hans control sessions took place immediately following the final block of sessions reported in Figure 2. Regular test sessions were resumed immediately following the final Clever Hans control session and maintained for approximately 500 additional trials.

Data Collection. All sessions were videotaped. Randomly selected sessions were scored by independent observers in order to confirm the accuracy of data recorded by the experimenter during each session.

RESULTS

As in our previous work with rats, performance was analyzed in terms of three categories: Eating fewer than, more than, or exactly the target number of food items. During most initial training and early test sessions, both subjects attempted to eat all the food available in the arrays on every trial. Over the course of subsequent sessions, the behavior of both subjects began to come under control of the numerical contingency. The progressive shift in modal responding to the target number is illustrated in trial blocks reflecting early, middle and final stages of testing (see Figure 2).

The use of negative social consequences revealed an initial between-subject difference in the ease with which eating "more than" the target number was suppressed. As shown in Figure 2, the male ferret was relatively insensitive to the occurrence of negative consequences and continued to take food beyond the third pellet. Throughout the first block of 80 trials, eating "more than" remained the male subject's modal response.

In contrast, the female ferret, who was generally more submissive in social interactions, was highly sensitive to the negative consequences of eating "more than" the target number. This sensitivity was so

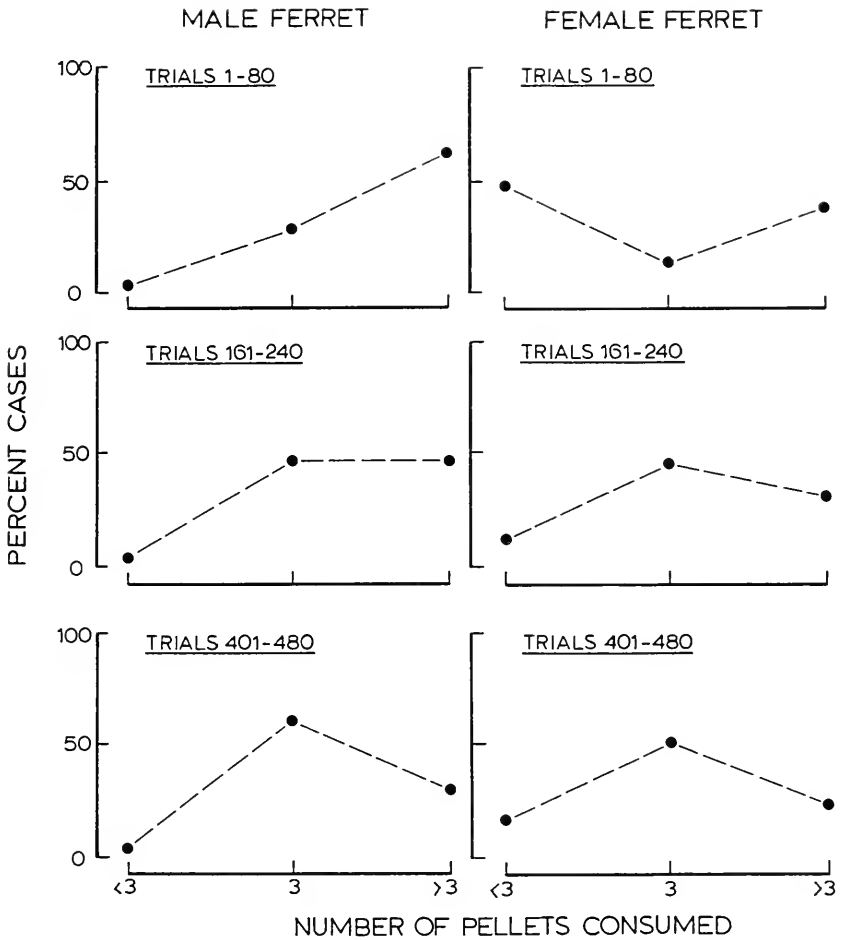

Figure 2. The percent of cases on which the male and female ferrets ate more than, less than, or exactly the target number of food pellets. Data are grouped into three trial blocks, recorded over the course of testing.

pronounced during early stages of testing that eating "fewer than" the target number was the female's most frequent response during the initial block of trials.

This difference between subjects was erased during the remaining stages of data collection shown in Figure 2. In general there was a sharpening of numerical control in both animals as the frequency of both "fewer than" (in the case of the female) and "more than" categories were substantially reduced. As illustrated in the figure, eating exactly the target number became the modal response for both subjects. Use of the binomial probability table to evaluate results of the final trial block

reveals significant performance ($p < .01$) for both subjects.[1]

The time taken to consume three pellets was examined in order to evaluate the possibility that performance was based upon a "rhythmic" pattern of eating, rather than a numerical discrimination. Rhythmic patterns require regularity in inter-pellet intervals, which result in relatively stable trial durations. Such was not the case for either animal. The distribution of successful trial durations for the data reported in Figure 2 (timed from initial contact with the first pellet to the third) showed sufficient variability to preclude a case for the use of "rhythm." (Male: mean trial duration = 37.6 sec; range 24-58 sec;. sd = 9; Female: mean trial duration 38.6 sec; range = 22-72 sec; sd = 12.6 sec.)

These data were further analyzed to determine whether the duration of correct trials differed from those on which fewer or more than the target number of pellets were consumed. If successful performance were based upon "rhythm," the consumption of pellets at a stable rate would yield differences in the durations associated with "fewer than," target number, and "more than" trials. However, a comparison of these three distributions for both the male and female subjects revealed no significant difference in the durations associated with these three outcomes. For the male ferret, trial durations averaged 35.4, 37.6 and 32 sec for "fewer than," target, and "more than" outcomes ($F = 1.78$; $p = .182$). For the female, trial durations averaged 35.3, 38.6 and 34.6 sec for the three outcomes ($F = .43$; $p = .656$).

The numerical nature of this discrimination was further underscored by the fact that individual food items varied in both shape and weight (range 130 to 286 mg), thus minimizing the potential contribution of volumetric cues. In addition, data from the "small pellet" control sessions revealed that performance was not affected, thus further minimizing the role of volumetric cues. Both subjects performed normally during these probe trials (3/4 correct on two consecutive sessions for the male subject; 3/4 and 2/4 correct for the female subject). Moreover, both subjects correctly consumed the target number during the initial two trials of the first control session.

In general, subjects followed no reliable foraging pattern either between trials or sessions. Food items were consumed opportunistically; i.e., subjects ate as they walked. Movement within the array showed

[1] Calculation of the binomial probability was based upon the conservative assumption that the three outcomes (eating more than, less than, and exactly the target number) were equally likely. Using this analysis, the binomial probability associated with the male's 61% correct responses (49/80 trials) when p/success = .33 equals less than 0.0001. The binomial probability associated with the female's performance equals 0.0007.

considerable variability, both in terms of the location of the first pellet consumed as well as the pattern followed once consumption began.

In order to examine whether numerical performance depended upon cuing by the experimenter, four Clever Hans control sessions were run. These data are summarized in Table 1. The important results of these sessions are that (1) performance did not depend on such cuing; i.e. correct responses were recorded even with the experimenter removed from the test enclosure. However, (2) the maintenance of correct performance did depend upon the threat of negative reinforcement.

During the critical first control session, both subjects ate the target number of food items on each of the first three trials. For both subjects, however, overall trial duration increased during the session, reaching unusually high values by the third trial (65 sec for the male; 72 sec for the female). Both animals engaged in extensive exploration (e.g. sniffing

Table 1. Performance of male and female ferrets during Clever Hans control sessions in which subjects were tested in the absence of feedback with the experimenter removed from the room. C indicates a Correct response. > indicates more than the target number of pellets was consumed. -- indicates that further testing was precluded because all remaining food items were consumed on the previous trial.

Control Session	Trial	Male	Female
1	1	C	C
	2	C	C
	3	C	C
	4	>	>
2	1	C	C
	2	C	C
	3	>	>
	4	>	>
3	1	>	C
	2	--	>
	3	--	--
	4	--	--
4	1	>	>
	2	--	--
	3	--	--
	4	--	--

the air) beginning late in the second trial and continuing throughout the third trial. The fourth trial consisted of a "more than" error by both animals.

During the second control session, both animals began with two correct trials, although the duration of trial # 2 was again extended by exploratory behavior. "More than" errors were recorded during each of the remaining trials in session 2.

During session 3, the female began with a correct trial. On the second trial there was considerable exploration prior to consuming the first pellet. The trial ended in a "more than" error. On the third trial, all remaining food items were eaten by the female. The male ferret began session 3 by slowly eating three pellets and pausing. Without returning to the start area, a fourth pellet was taken. The subject then paused, and consumed all remaining pellets on the plank, periodically rearing up and sniffing.

By the final Clever Hans control session, the performance of both animals reverted to its original pretraining level; i.e. all pellets were consumed on the first trial. Evidence from the sessions that immediately followed strongly suggests that this deficit in performance was motivational. When normal testing conditions (including the use of negative consequences) were resumed, discriminative performance was reestablished to pre-control levels by the end of the third post-Clever Hans session.

Although performance stabilized during the final trial block reported in Figure 2, additional testing was undertaken for both subjects. Rather than sharpening behavioral control, these additional sessions revealed a progressive deterioration in performance. It was clear at this point that the negative consequences had ceased to be an effective controlling stimulus. When testing was terminated following approximately 1000 trials, eating "more than" had become the dominant response for both subjects (66% for the male; 45% for the female during the final block of trials). Overall accuracy levels fell to 26% and 39% for the male and female ferret, respectively.

DISCUSSION

There are three important aspects of these data. Firstly, the progressive shift in modal frequency to the target number shown in Figure 2 and, in particular, performance levels reported in the third trial block. These data confirm that ferrets are capable of numerically restricting their food intake. The results are essentially similar to those

previously demonstrated with this procedure using rat subjects (Davis & Bradford, 1991), as well as those originally reported with budgerigars by Marold (1939). It should be stressed, however, that ferrets required more than twice as many trials as rats to suppress competing responses and yield modal levels of correct responding.

Secondly, as in our previous report with rats, the various control procedures suggest that performance was essentially numerical in nature and did not depend upon pellet size, volume, foraging pattern, or rhythmic cues. The data from the "Clever Hans" control sessions are of particular importance. There is a clear similarity between the present results with ferrets and those previously reported with rats (Davis, 1989; Davis & Bradford, 1991). The results of the first "Clever Hans" control session merit special attention. The maintenance of correct responding by both subjects during the initial trials confirms that performance does not depend upon cuing by the experimenter.

The deterioration of performance that occurred during subsequent control sessions does suggest, as it did in the case of rat subjects, that the threat of negative consequences rather than cuing was essential to maintaining performance. With rats and ferrets alike (no such controls were run in the study with budgerigars), the change in experimental conditions prompted considerable investigation by the animals (e.g., rearing up, sniffing). Once subjects detected that the aversive reinforcement contingency had been suspended, performance reverted to pre-training levels. The ease with which correct performance was reintroduced in both species when negative consequences were reinstated suggests that the transient failure observed during control sessions was essentially motivational in nature.

The necessity of aversive control to maintain discriminative control also bears upon the third important aspect of these data: the ultimate deterioration of performance after stability was attained. Because neither rats nor budgerigars were subjected to such additional testing (c.f., Davis & Bradford, 1991; Marold, 1939), we do not know whether their performance would have shown similar deterioration. In the present case, observation of experimenter-subject interactions during this period suggests that neither animal was as intimidated by the delivery of negative consequences as it had been earlier in testing (Davis & Balfour, 1992). Whereas "threats" (e.g., shouting, handclapping) had previously suppressed undesirable behavior, these consequences had virtually no effect on either subject during the final stages of testing. Only direct physical contact with the animal appeared to alter its behavior, and the effectiveness of this approach, itself, was inconsistent. Thus the ethically appropriate low levels of aversive consequences that we used were

insufficient to consistently suppress behavior. There are similar reports by a number of Koehler's (1950) colleagues (Wesley, 1961). In any case, when the efficacy of punishment declined in the present situation, performance of both ferrets deteriorated dramatically.

Although this account places a large emphasis on the suppression of competing responses, it should be stressed that aversive control alone could not have resulted in successful performance. In short, negative consequences are a necessary, but not sufficient ingredient for successful performance. Without the underlying ability to discriminate the quantity three, the threat of events alone would not yield the success reported with this procedure (see also Marold, 1939; Davis & Bradford, 1991).

Are ferrets truly "headstrong" and therefore relatively poor subjects in laboratory learning situations (e.g. Pollard & Lewis, 1969)? Such judgments should be tempered by the fact that competing responses in the present situation were essentially consummatory in nature. Their probability may have been raised by our use of food deprivation (albeit low level by conventional standards), as well as the presence of freely available food. It has been argued (e.g., Davis & Shattuck, 1980; Decosta & Ayers, 1971) that consummatory behavior may be harder to suppress than the arbitrary instrumental acts typically employed in numerical testing (e.g., Boysen & Berntson, 1989; Davis, 1984; Fernandes & Church, 1982).

In summary, ferrets, like rats, show evidence of numerically restricted food intake only as long as there is ample reason to do so. Both species clearly revert to pretraining consummatory levels when the threat of negative consequences is temporarily suspended during control sessions (Davis, 1989), or when it ceases to be a deterrent. Insofar as numerical competence, especially involving absolute quantities, has little to do with success in the natural environment, it is arguably adaptive to abandon learned behavior when the cost is low, in favor of more opportunistic foraging strategies. General statements about a species' "trainability" or its potential for numerical competence should be tempered by such considerations.

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VIIIth BIENNIAL MEETING OF THE INTERNATIONAL SOCIETY FOR COMPARATIVE PSYCHOLOGY

Monteal, Canada, August 14-16th, 1996

ABSTRACTS OF PAPERS IN SYMPOSIA

FLEXIBILITY AND EXPERIENCE IN INVERTEBRATE BEHAVIOUR

Cesar Ades, Organizer

Invertebrate behavior is more than fixed species-specific patterns of performance. The purpose of the symposium is to explore, using as case studies the reproductive behavior of stingless bees, locomotor orientation in isopods and web building by orbweb spiders, aspects of the variability and learning in so-called simple systems. The use of invertebrate models contributes greatly to our understanding of the way pre-programs and experience integrate in behavior and raises a host of relevant issues from a comparative point of view.

BEHAVIORAL FLEXIBILITY IN MALE PRODUCTION BY WORKERS IN THE STINGLESS BEE MELIPONA BICOLOR *(APIDAE MELIPONINAE). Vera Lucia Imperatriz-Fonseca, University of Sao Paulo*

Stingless bees are eusocial bees with massive brood cell provisioning. In most of such bees, trophic workers eggs (TWE) are offered to the queen during cell provisioning. The queen's control of worker reproduction is probably related to a second kind of egg (WRE) which is delivered by the worker when closing the cell, after queen oviposition, and which gives origin to male individuals. Melipona bicolor is a species that has more than one fertilized queen simultaneously in the colony: social conflicts among queens increase the

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Address enquires regarding this meeting to Nancy Innis, Department of Psychology, University of Western Ontario, London, Ontario, N6A 5C2 Canada.

possibility of worker reproduction and generate a remarkable behavioral variability. During WRE cycles, large courts are paid to the queens, with bouts of aggressive behaviour (as antennation) among queens, competition among workers in cell sealing, workers antennation and policing over the reproductive worker, cell manipulation after its complete sealing followed by oophagies and a new WRE oviposition. Cells are strongly defended by the reproductive worker. WRE are concentrated in some cells which are recognized among others by the workers and by the queens. The behavioral flexibility observed in this phase can be due to special aspects of social context and is influenced by kinship relationships and probably by a pheromone-based balance process.

MEMORY FOR PREVIOUS TURNS IN INVERTEBRATE ALTERNATION BEHAVIOR *Robert N. Hughes, University of Canterbury*

The tendency to alternate turns at successive obstacles while walking characterizes a wide range of bilaterally symmetrical invertebrates. The phenomenon enables corrections to be made for deviations from a linear path of movement thereby facilitating foraging, escape and dispersal of the species. As the direction of each alternating turn depends on stored information about a previous turn or sequence of turns, there have been several explanations provided to account for this. The most popular during the last 40 years have been reactive inhibition, and thigmotaxis accompanied by centrifugal swing. Of these two, it is only reactive inhibition that emphasises responses based on information stored about preceding responses. While the tendency amongst some researchers has been to determine which explanation is the "correct" one overall, it is more likely that either might be more or less appropriate depending on specific alternation settings and species. A variant of the reactive inhibition-type approach has involved the possibility that information about earlier turns might be acquired and retained through movements of legs involved in the execution of a turning response. It might therefore be that memories for the direction of earlier turns reside in the peripheral neural controlling mechanisms of the legs themselves. Research bearing on this issue will be described in which the involvement of specific legs in turning and then turn alternation has been investigated in the terrestrial isopod, *Porcellio scaber*.

SINCE INSTINCT CAN BE LEARNT: FLEXIBLE ASPECTS OF ORB-WEB BUILDING *Cesar Ades, University of Sao Paulo*

Orb-web building is generally taken to be a highly specific,

stereotyped, resistant-to-learning activity. I present three studies with the tropical orb-weaver *Argiope argentata* (*Fabricius*) which provide information about the possibility that web building is modulated by subtle environmental aspects; and that it is, under special circumstances, influenced by past experience. In the first study, spiders in square, vertical wooden frames could rebuild their webs either in an undisturbed context, or after a 180 degree rotation of the frames, which inverted the normal up/down asymmetry of the web (larger radial lines now at the top of the web). Webs rebuilt in a "rotated"condition were structurally different from webs in the control condition, a result which indicates that, during removal and replacement, spiders may be guided by structural relationships of the old web. In a second study, groups of spiders which had each spent a long period in different-sized frames (constructing webs proportional in size to the available frame) were transferred to smaller, bigger or equally sized frames. Previous building experience did not affect web structure. Experience effects were, however, demonstrated in the third study, in which spiders were induced to build, successively, in vertical and horizontal frames. Performance was disrupted the first time spiders built in the horizontal (a quite unnatural context): constructions varied from a totally irregular array of lines to webs with different degrees of completeness. Continued exposure to the horizontal condition led to a persisting improvement in building quality.

THEORETICAL AND METHODOLOGICAL CONSIDERATIONS IN THE STUDY OF EXPLORATORY BEHAVIOR

Robert Hughes, Organizer

INTRINSICALLY-MOTIVATED EXPLORATORY CHOICE PREFERENCES

Robert Hughes, University of Canterbury

In many empirical studies of exploratory behavior in nonhuman animals there is still insufficient attention paid to the distinction between extrinsically and intrinsically motivated forms of the phenomenon. This is reflected in the type of measures adopted and the conclusions drawn especially when assessing effects of experimental manipulations, such as brain lesions and drugs. While extrinsically-motivated exploratory behavior involves seeking specific goals unrelated to the behavior itself (such as food or shelter), intrinsically-motivated forms are said to "occur for their own sake" since they are reinforcing in their own right. Intrinsic exploration is more popularly described as "curiosity behavior" and assumed to arise from some investigatory motive or propensity for

animals to be curious about their environment. Historically, curiosity-related behavior was ascribed firstly to the operation of secondary hunger or primary exploratory drives and then later to attempts to maintain optimal levels of CNS arousal. Although these explanations had some intuitive appeal, they did little more than restate the fact that many animals show a tendency to EVENTUALLY approach and explore novel or unusual stimuli seemingly unrelated to the satisfaction of any specific need (other than a possible need to experience sensory stimulation). Attempts to measure intrinsic exploration must take account of those stimulus qualities believed to arouse and reinforce the behavior. In this respect, choice preferences will be discussed in comparison with activity indices, responses to complexity and sensory reinforcement.

THE OPEN-FIELD TEST: FAILURES AND PROMISES *Gary Greenberg, Wichita State University*

In 1994 I began to draw attention to the continuing need for standardizing the open-field test, one of the most widely used test procedures in comparative psychology. This test, in which animals are placed in a novel environment for brief periods, is widely held to indicate levels of emotionality. This current review criticizes the validity of these procedures for assessing emotionality particularly given the extensive degree of procedural variability that characterizes the use of the open-field today. Data are presented bearing on the need for developing a standard methodology for the use of the procedure. A multinational collaborative research effort among Wojtek Pisula of Poland, Bryan Jones of Scotland, and the present author, addressing these points will be described.

INDIVIDUAL DIFFERENCES IN EXPLORATION: A MULTIVARIATE APPROACH *Wojciech Pisula, University of Warsaw*

Fifty five rats were tested in an exploration box. The 484 basic sequences of behavioral acts were taken. Hierarchical cluster analysis was performed. Basic behavioral patterns employed by the rats were identified. The analysis of the patterns revealed both quantitative and qualitative differences in rat behavior. Results are discussed in terms of individual differences in temperamental characteristics in rats and motivational mechanisms underlying stimulus-seeking behavior.

A THEORETICAL MODEL OF EXPLORATORY BEHAVIOR *Jan Matysiak, University of Warsaw*

Considering the important role played by adaptation to the

environment, it is necessary to recognize the primacy of motivation for exploratory behavior, among other motives of organisms. This view is not a very original one since Woodworth (1958) already stated that a tendency to cope with the environment is a primary motivation of behavior, and to fulfil other organic needs - secondary goals. A proposed theory of need for stimulation attempts to explain motivational mechanisms of exploratory behavior. On the basis of results obtained in our laboratory, it seems necessary to include in our previous concept (Matysiak, 1980) a hypothetical construct explaining the participation of emotions in the process of motivation of exploratory behavior. The modified theory satisfactorily explains motivational mechanisms of exploratory activity as well as empirical facts of the existence of two phases of activity, transpiring from our results. Moreover, the many times described sensory reinforcement phenomenon (Kish, 1966; Matysiak, 1985) also derives its explanation, becoming a significant element of the theory.

THE INTERSECTION OF THEORY AND METHOD IN THE STUDY OF EXPLORATION AND CURIOSITY *Michael J. Renner, West Chester University*

One approach to examining the study of exploration and curiosity is to examine the open field test as it is commonly administered, and evaluate the type of behavior that is typically elicited by this procedure. An alternate approach is to have some target behavior -- or behavior system -- in mind and alter the open field situation (apparatus and procedure) to make the expression of such behavior likely. This paper will discuss the evolution in my laboratory of techniques designed to allow and encourage subjects to emit spontaneous investigatory behavior (often called "curiosity") and consider the ways in which this modified situation is like and unlike the typical open field test. Many modifications to the prototypical open field situation change the stimulus field presented to the subject and therefore the character of the behaviors elicited therein. These include remote video observation, low-light conditions, pre-exposure to the arena and procedure, minimization or elimination of handling by the experimenter, and the presence of novel and familiar stimulus objects in the field. Although each of these may change the situation in such a way that other investigators may say "this is nice, but it's no longer an open field test" the issue is semantic. If the open field test is solely for assessing stress or emotionality, and perhaps fear-induced locomotion, these criticisms are valid. If the open field is simply a neutral context for examining spontaneous behavior, then it can reasonably be modified for different experiments to assess different

aspects of behavior. Some types of behavior are not (yet?) amenable to automated study. This paper will provide examples of such behaviors, such as a grammar-like sequential structure in spontaneous investigatory behavior, and argue that an open-field situation, or something very much like it, is the only empirical method by which such discoveries could be made.

VIDEO-PLAYBACK AND ITS ROLE IN ANIMAL BEHAVIOUR RESEARCH

Bryan Jones, Organizer

Investigating animals' responses to video images could present exciting opportunities to improve our understanding of the way they perceive and regulate their physical and social environment. Not only are the results of such studies likely to be of fundamental importance in the areas of cognition and communication but they may also have strategic relevance. For example, they may guide developments in animal housing and husbandry. The technology is now available and responsiveness to video stimuli has been documented in a wide variety of species. This symposium focuses mainly on a range of species from fish to baboons. Current advances will be reported, the potential benefits and limitations of video stimulation will be discussed, and directions for future research will be identified.

VIDEO DISPLAY AS A STIMULUS PRESENTING DEVICE FOR BIRDS *Shigeru Watanabe, Keio University*

We are studying pigeons' responses to diverse video displays. Firstly, for example, the stripe stimuli created by a video pattern generator are displayed on a high resolution TV monitor in order to measure visual acuity. When a pigeon places its head at a specific position in an operant chamber, a blank and a stripe stimulus of equal brightness appear on the screen. Pecking the stripe stimulus produces food reinforcement. Secondly, visual stimuli can be easily modified using computer software such as PHOTOSHOP. We trained pigeons to discriminate between still images of pigeons and Java sparrows, different people, and different cartoon characters. We then displayed scrambled or incomplete video images. The birds discriminated scrambled cartoons but their discrimination of scrambled pictures of birds or people was comparatively poor. Thirdly, we trained pigeons to discriminate between two moving images (words of Japanese Sign Language). Finally, people can easily identify human motion by watching the movement of a few

illuminated dots on an image of the body (Johannson's stimuli). We showed that pigeons could also discriminate movement of dots pasted on to a pigeon and a toy dog. Potential problems of using video displays will also be discussed.

VIDEO PLAYBACK EXPERIMENTS: PROBLEMS AND PROMISES *Christopher Evans, Macquarie University*

Video playback experiments have the potential to provide new insights into the way animals process visual stimuli. Insects, arachnids, lizards, fish, birds and primates are all responsive to video stimuli. By using digital image-processing techniques we can now produce high-quality sequences that permit increased control over stimulus attributes and the creation of otherwise unobtainable stimuli. Technical obstacles that had limited the quality and realism of video sequences have largely been overcome and we can now even engage in interactive playback experiments with our animal subjects. These exciting advances suggest a program of experiments modelled on the acoustic playback studies that yielded so much valuable information about auditory signals. However, video playbacks are not a panacea. There are obvious concerns about species differences in visual system characteristics and, particularly in sensitivity to wavelengths not reproduced by video monitors which have been designed for the idiosyncrasies of human colour vision. Careful consideration of such constraints suggests that the video playback experiment is a very powerful tool, but one which should be applied selectively.

HOLLYWOOD FARM: DOMESTIC CHICKS' RESPONSES TO SYMBOLIC VIDEO IMAGES *Bryan Jones, Roslin Institute (Edinburgh).*

Assessing chickens' reactions to video images may improve our understanding of the way they perceive and regulate their environment. This, in turn, may guide the development of effective environmental enrichment devices. Chicks were housed individually (Study 1) or in trios (Study 2) and received brief daily exposure to either a simple (blank monitor) or a complex (screensaver) video presentation. A series of experiments carried out within each study examined the development of approach/avoidance responses with repeated exposure as well as the chicks' subsequent preferences for familiar or unfamiliar video images in a two-choice situation. Two main conclusions were reached. Firstly, the results of both studies illustrated the attractive nature of video images and of component features such as stimulus complexity and moderate novelty. Secondly, they suggested that the opportunity to form filial

attachments did not prevent the chicks from becoming attracted to symbolic video images.

THE USE OF VIDEO-PLAYBACK FOR STUDYING SOCIAL BEHAVIOR IN FISHES *Bill Rowland, Indiana University*

Many fishes are sensitive to relatively simple visual cues and video-playback is effective for studying complex social behavior. Our laboratory uses video-playback to study visual aspects of aggression and courtship in threespine sticklebacks. By manipulating color, movement, speed, and other features of video-taped images of live fish or computer-simulated animations of them, we investigate the importance of these features in fighting, mating and other behavior. We have also conducted preliminary playback experiments on the jewel cichlid and the Siamese fighting fish. Our results, as well as some applications and limitations of video playback, will be discussed.

A VIDEO TASK TO STUDY COGNITIVE PROCESSES AND HEMISPHERIC SPECIALIZATION IN BABOONS *J. Vauclair & J. Fagot, C.R.N.C, C.N.R.S.*

We designed a video task requiring the manipulation of a joystick to study Guinea baboons (*Papio papio*). Three aspects of this technique will be considered: 1) The training phases in the mastery of the task by the monkeys; 2) The presentation of the different experimental procedures (GO/NOGO, identity and arbitrary matching to sample) and their use in the investigation of several cognitive processes in non human primates; and 3) An illustration of the successful application of the task for studying hemispheric specialization in intact baboons. The latter work suggests that purely behavioral methods can constitute reliable alternatives to traditional physiological approaches.

PERSPECTIVES ON HUMAN-ANIMAL INTERACTIONS

Emily Weiss, Organizer

A brief overview of the various Human-Animal Interactions (HAI) in science, industry, and everyday life, with an emphasis on the research in these areas will be presented.

APPLIED HUMAN-CANINE INTERACTIONS *Al Prestrude, Virginia Polytechnical Institute*

There are three factors that contribute to the unique relation between dogs and humans. Dogs have a long evolutionary history leading to a

high degree of socialization which led to it being the first domestic animal over 10,000 years ago. Its adaptability has resulted in over 400 breeds specialized for a wide variety of tasks, but dogs still maintain their fundamental canine character. The sensory capabilities of dogs are among the most acute in the animal kingdom. The combination of loyalty, adaptability, and sensory acuity has made the dog one of humankind's most useful animals. I will review several activities in which dogs provide unique services to humans including our current work with dogs as detectors of hazardous materials.

THE INEVITABLE IMPACT OF SCIENTIST-ANIMAL INTERACTIONS ON THE RESEARCH PROCESS *Hank Davis, University of Guelph*

Scientists and animals interact daily in a variety of research settings. There is a growing body of evidence to suggest that these encounters, in which specific humans are reliably paired with hedonic events, have measurable impact on animal subjects. Behavioral and biomedical research is not immune to such effects. My talk is based on a recent book (The Inevitable Bond, Davis & Balfour, 1992) which suggests we can 1) minimize such disruptive or confounding effects on our research, and 2) use scientist-animal interactions to maximize subject motivation and enhance the research process.

INTERSPECIES EPIPHANIES TRANSFORM THE HUMAN WELTBILDAPPARATUR *Anthony L. Rose, The Biosynergy Institute*

The perceptual apparatus that governs a person's world view (weltbildapparatur) is affected significantly by life experience with other species. During the past three years the author has collected and analyzed reports of hundreds of profound interspecies events (PIEs) that have altered the world views of lay people and wildlife professionals.. These events cluster into groups of similar epiphanies that reflect the relational processes of the humans involved. Among lay people and animal caretakers, the predominant interspecies epiphany is the interactive/humanistic type, in which animals Seek A Friendly Encounter with a human (the SAFE scenario). Experimental researchers tend to report PIEs modulated by detached objective processes that reinforce scientific values. Environmentalists describe more interpretive broad brush peak experiences reflecting naturalistic values. While these distinct epiphanies all shift a person's world view from anthropocentric to biocentric, they also energize interpersonal differences that produce social conflict. If science and conservation are to gain needed public support, researchers and environmentalists must understand and honor

the humanistic interspecies epiphanies that are most likely to transform the Weltbildapparatur of the common person.

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VIIIth BIENNIAL MEETING OF THE INTERNATIONAL SOCIETY FOR COMPARATIVE PSYCHOLOGY

Monteal, Canada, August 14-16th, 1996

ABSTRACTS OF PAPERS

CEREBRAL SPECIALISATION IN THE CHICK: NEW EVIDENCE FROM CHOICE OF IMPRINTING OBJECT *Richard J. Andrew, University of Sussex*

Domestic chicks which have imprinted to a ball, on the face of which is a horizontal bar, show choice according to bar orientation in tests in which the left eye is in use, but not when the right is in use (Vallortigara and Andrew, 1991, Anim. Behav., 41:187-194). Moderate change is chosen over the home cage pattern whilst large change is avoided. I have now found that right-eyed birds will choose when (for example) there is change in shape, rather than in internal features. The two hemispheres differ in the priority which they set on different properties of the stimulus. The data will be discussed as providing further evidence for the existence in birds of features of lateralisation, which have been described for humans.

AN INVESTIGATION OF ODDITY CONCEPT LEARNING IN RATS *Aileen M. Bailey and Roger K. Thomas, The University of Georgia*

Previous investigations purporting to show oddity concept learning in rats have been methodologically flawed. The present study tried to improve upon previous attempts to study oddity concept formation using olfactory oddity discriminanda. Despite our using an arguably too conservative measure of chance, one of four rats had three runs of better than chance performance on the first trials of new problems. All rats performed better than chance and highly successfully on trial 2 of new problems showing successful learning set formation. Results are discussed in terms of the necessity to distinguish between learning set

formation and oddity concept formation in nonhuman animals as well as again underscoring methodological problems that have plagued nonprimate investigations of oddity concept formation and use.

FRIEND, FOE, OR SELF? EVALUATION OF INTERACTIVE BEHAVIORS WITH MIRRORS IN THE BUSHBABY (*OTOLEMUR GARNETTII*) *Michelle L. Becker, Sheree L. Watson & Jeannette P. Ward, The University of Memphis*

Videotapes of 45 bushbabies exposed to novel stimuli were examined. The evaluation focused on behavioral interactions with the animals' own reflections in two mirrors. Behaviors examined include threatening postures, scent marking, and social behaviors, such as touching and licking the mirrors. Descriptive data are presented as well as analyses of the group effects of sex and age. Implications of temperament disposition are also discussed.

THE INFLUENCE OF THE MALE CALIFORNIA MOUSE (*PEROMYSCUS CALIFORNICUS*) ON PUP SURVIVAL AND FEMALE REPRODUCTIVE SUCCESS *Richard E. Brown and Debora Cantoni, Dalhousie University*

The California mouse is a monogamous rodent in which the male shows a high level of parental care. In our experiments, these mice were required to "forage" for food by running in a wheel. Male-female pairs could rear larger litters of pups to weaning more successfully than females alone, and the pups with both parents grew faster. Single females who reared their pups to weaning had a longer inter-birth-interval than paired females. Our presentation will discuss the behaviour of the male which increases pup survival and facilitates implantation in the female.

LATERALIZED RESPONSES TO VOLATILE STIMULI *T. H. J. Burne, University of New England*

Lateralized olfactory responses have been reported for a number of species including humans and the domestic chick. A right hemisphere (right nostril) advantage has been found for some odours but not others. Also, lateralized responses have also been reported for volatiles which stimulate the trigeminal system. This paper discusses the relative importance of lateralizations in the olfactory and trigeminal systems. I was able to elicit lateralized responses with a range of volatiles in chicks that had one or other nostril temporarily occluded. A comparison will be made between lateralizations in birds and mammals.

THE LEFT AND RIGHT OF MEMORY IN FOOD-STORING BIRDS
N. S. Clayton, University of California, Davis

Food-storing birds have evolved a remarkable feat of memory: they hide hundreds to thousands of food caches and rely on their memory to retrieve their caches when they return hours to months later. Monocular occlusion was used to investigate differences between the left and right eye-systems in memory processing by comparing food-storing and non-storing species. In food-storing marsh tits, information coming in to the brain from the left eye disappears from the left eye system between 3 and 24 h after memory formation and becomes accessible to the right eye system, whereas that coming into the brain from the right eye remains stable within the right eye system for at least 51 h after memory formation. In a closely related species that does not store food, the blue tit, the left eye system also differed from the right eye system as in marsh tits. However, unilateral transfer was found only in marsh tits, suggesting that there may be a difference between storers and non-storers in the mechanism of memory processing. Lateralization was also found at the molecular level, in the expression of the proto oncogene c-fos. Further experiments tested whether or not the two eye systems preferentially respond to different aspects of the stimulus. Two storer/non-storer pairs of species, marsh tit/blue tit and jay/jackdaw, were compared on a one-trial associative learning task. The results of the latter experiment suggest that food-storing birds differ from non-storers in responding preferentially to spatial information and that in storers and non-storers the right eye system shows a preference for object-specific cues and the left eye system for spatial cues.

THE OBLIQUE EFFECT IN PIGEONS *Francisco J. Donis, Central Connecticut State University*

The oblique effect was investigated in two experiments. In Experiment 1, four subjects (Group 1) were trained to discriminate between two oblique lines presented successively on the screen of a computer monitor, and 4 subjects (Group 2) were trained to discriminate between horizontal and a vertical lines. These stimuli were white presented on a dark background. The results show that the performance of subjects in Group 2, as measured by proportion correct and reaction times, was superior than that of subjects in Group 1, although only the superiority in reaction times was maintained throughout the 60 sessions of training. In Experiment 2, five subjects were trained to make the two discriminations given to the two groups in Experiment 1. Although these results show a weak oblique effect, they are not as clear as those of Experiment 1. The results of the study are discussed in terms of biasing

habitats in which lines in the orientations of the main axes predominate.

SIGNS OF DEVELOPMENT IN CHILDREN AND CHIMPANZEES
R. Allen Gardner, University of Nevada, Reno

In cross-fostering, adults of one genetic stock rear the young of another genetic stock to study the transmission of behavior across generations. True cross-fostering is a rigorous, 24-hr per day, 7 days per week, procedure. Slides and discussion of Project Washoe and its replication with the infant chimpanzees Moja, Pili, Tatu, and Dar, illustrate childlike development of infant chimpanzees using sign language as well as household objects such as mirrors, crayons, pens, and eyeglasses

A NEW ANIMAL MODEL FOR SPACE RESEARCH: THE GERBIL
Gary Greenberg, Wichita State University

Research in the space environment has involved animals from the inception of the space program: dogs, chimpanzees, and currently, rats. We propose the gerbil is a more appropriate model than the rat. They weight less, eat and drink less, defecate and urinate less. The gerbil has become an important model for medical research. We report data on activity patterns in gerbils exposed to Light/Dark cycles experienced by astronauts engaged in extravehicular activity such as involved in repairing Hubble telescopes and building space stations. Our data show that this exposure depressed activity in gerbils suggesting that human performance in orbital flight may be similarly affected.

MENTAL ROTATION IN PIGEONS? *Jeff Hamm, W. R. Matheson, & W. K. Honig, Dalhousie University*

Pigeons discriminated between singly presented upright line drawings of six pairs of objects (e.g. zebra positive vs. tiger negative). In testing, the drawings were presented in six orientations. With increasing rotation from the upright, the discrimination declined. This effects corresponds to data on mental rotation in humans.

CIRCADIAN CONTROL OF DUSTBATHING IN JUNGLEFOWL
Jerry A. Hogan and James Perretta, University of Toronto

Junglefowl on a 12:12 hr light:dark cycle show a marked peak of dustbathing in the middle of the light period. Four experiments were done: 1) light onset and offset were advanced by 3 hours, 2) onset and offset were delayed by 3 hours, 3) onset was advanced and offset delayed by 3 hours [giving an 18:6 light:dark cycle], and 4) onset was delayed and offset advanced by 3 hours [giving a 6:18 light dark cycle].

In experiments 1 and 2, the peak of dustbathing moved about an hour a day toward the middle of the new light period. In experiments 3 and 4, the peak of dustbathing remained steady in the middle of the light period. The results are all consistent with the hypothesis that dustbathing is partially controlled by a circadian clock.

TRANSPOSITION OF RELATIVE NUMEROSITY DISCRIMINATIONS IN PIGEONS *W. K. Honig & W. R. Matheson, Dalhousie University.*

Pigeons were trained to respond differentially to the two sides of randomized arrays, when two different proportions of colored elements were presented. The discriminations were transferred relationally or nonrelationally to other pairs of proportions. Relational transfer was immediately obtained under both conditions, even though this was incorrect for the nonrelational group.

EYE PREFERENCES AND AROUSAL IN THE COMMON MARMOSET (*CALLITHRIX JACCHUS*) *M. Hook-Costigan and L. J. Rogers, University of New England*

Despite increasing interest in the study of functional asymmetries in nonhuman species, research on perceptual (as opposed to motor) asymmetries has been sparse. Therefore, we examined eye preference in the marmoset to determine if, like humans and the small-eared bushbaby, the common marmoset displays lateralisation for this function. Age and stimulus effects on eye preference were examined by scoring the eye preferred to peep through a small hole. We found a strong bias within the group for right-eye preferences when viewing neutral stimuli (18 of 19 marmosets displayed significant right-eye preferences). However, arousal induced by a fearful stimulus led to a shift away from right eyedness; of the 9 marmosets that have displayed a fear response, 3 were left-eye preferent, 1 preferred the right eye and 5 displayed no preference for either eye. Approximately 70% of humans are right-eye preferent, some researchers claim that left-eye preferences occur more frequently amongst people diagnosed with alcoholism and schizophrenia. The researchers have proposed that a greater incidence of left-eye dominance may reflect a biologically determined difference of cerebral dominance but, in light of the evidence found for the marmoset, we suggest that left eyedness may simply reflect different levels of arousal in the testing environment. The relationship between eyedness and other motor functions in the marmoset, such as hand use and asymmetry of facial expression, will be discussed.

FUNCTIONAL ASYMMETRY IN THE CHICK *Amy N. B. Johnston University of New England*

Studies using chicks have shown that lateralized brain functioning is particularly important for learning and memory. Birds are excellent models for exploring lateralized brain function as there is a complete decussation of the optic nerves and, compared to mammals, relatively few interhemispheric connections. This paper will describe a series of experiments which demonstrated disruption of memory recall following the administration of glutamate into the right forebrain hemisphere, but not following the administration of glutamate into the left forebrain hemisphere. These experiments also addressed the issue of whether the effects of lateralized glutamate administration were due to altered monocular viewing preferences or to disrupted recall per se. By assessing monocular viewing preferences following unilateral glutamate administration it is possible, to a large extent, to dissociate asymmetrical recall and lateralized viewing preferences. In the chick, it has been possible to demonstrate clearly lateralized memory processes.

ON CATEGORIZATION THROUGH MOTIVATIONAL MECHANISMS *Faisal L. Kadri, Sarnia, Ontario*

Motivational models of behaviour are numerous yet the interest of academics to study them is small, consequently there is little expectation of practical and useful results from a validated model. This is an example of a recently introduced nonlinear model of motivation and its potential to answer important questions such as: Could a mechanism of priming/ regulating behaviour produce motivational categories? How? How many? And: What could a motivational model tell us about cognition and cognitive vs. motivational categorization? The answers, if and when the model is experimentally validated, can be far reaching.

SELECTIVE ATTENTION AND MIMICRY IN THE AUSTRALIAN MAGPIE Gisela Kaplan, University of Queensland

There exists a large body of literature on song development and mimicry in avian species of the northern hemisphere. Very little work has been done to date on the independent development of song and mimicry in avian species of the southern hemisphere. The Australian magpie (*Gymnorhina tibicen*) is capable of complex vocalisations, including mimicry of dogs, horses and other avian species. Such mimicry, and the development of mimicry, has been recorded for the first time throughout the first year of life (from fledgling, juvenile to adult). The paper will focus on the selective attention to specific stimuli within the social/territorial context.

GROUND ROOSTING IN DOMESTIC FOWL (*GALLUS GALLUS DOMESTICUS*) IN THE GAMBIA, WEST AFRICA: THE ROLE OF LIGHT LEVELS *J. P. Kent, A. G. McElligiott & H. V. Budgey, University College, Dublin*

The ground-roosting behaviour of a semi-feral population of domestic hens with broods of chicks was measured in The Gambia, West Africa. Although neither day length nor time of sunset changed significantly over the duration of the study (January -March 1995), daylight intensity showed a significant increase. This resulted in an increasingly rapid decline in light intensify at dusk as the season progressed. Hens went to roost significantly later in the day, and at decreasing light levels, as the season progressed. The results suggest that the cue to start roosting is a certain light level, constant over the season, but that the settling period required means that the hens finally roost at later times and lower light levels as the season progressed.

FIRST STEPS IN COMPARATIVE ANIMAL EDUCATIONAL PSYCHOLOGY *M. Kiley-Worthington & H. D. Randle, University of Exeter and University of Plymouth*

Animal educational psychology ("animal training"), the comparative study of animal handling and learning, has not to date attracted any serious research attention. This is a science whose promotion and cultivation is long overdue, given the growing importance of human-animal interaction. Studies of animal cognition are now being published by both cognitive ethologists working on wild populations and cognitive psychologists working on laboratory animals. However, there is another approach, involving close student-teacher interaction: Animal Educational Psychology. This approach asks not only what can animals learn when in their own or highly controlled laboratory environments, but also what can they learn to do through interaction with a human teacher. Some recent studies have thrown severe doubt on the assumption that as we have been training domestic species for so long we have already found out the best way to do it. "Preconceived beliefs" and "folk-psychology" are identified as controlling developments in this area. This paper describes the preliminary findings of teaching 5 subjects of 4 different domestic species (equine, bovine, canine and camelid) simple tasks (moving body parts on command), complex tasks and manipulative tasks. Preliminary analysis of the behaviour of both the subject and the teacher provides an assessment of first, the effects of using positive reinforcement, second, the speed of learning verbal cues, and third, the use of other aids during teaching (including gestures,

restraint and imitation). Despite the small sample, the degree to which the species differences fulfil the "folk-psychological" beliefs surrounding these species can be discussed. This paper also addresses the importance of both procedural and declarative knowledge.

THE ROLE OF HEARING IN VOCAL PRODUCTION AND VOCAL LEARNING IN BUDGERIGARS (*MELOPSITTACUS UNDULATUS*) *Kazuchika Manabe & Robert Dooling, University of Maryland*

Several experiments examined the effect of masking noise and temporal hearing loss on the maintenance of learned species-specific vocalizations in budgerigars. These results show that budgerigars monitor each production of their learned vocal signals through auditory feedback, and that interfering with this feedback results in immediate changes in the structure of these calls. These results suggest stronger parallels with human vocal learning than other avian models of vocal learning.

MAXIMISING PERIPHERAL VISION WITH MINIMAL EFFORT -A NEW FOCUS SYSTEM IN BIRDS *S.A. McFadden and K. Rounsley, University of Newcastle, Australia*

Lateral eye position has the advantage of affording a panoramic view of space but has the consequence of only peripheral optics being available for frontal vision. In birds, this is offset by good peripheral optics and the evolution of multiple specialisations to subserve different parts of space. However, this alone is not enough, as an eye also needs to focus at a range of distances and the usual mechanism of accommodation of the lens may not be sufficient within the frontal field. We have found that the pigeon uses an entirely different strategy to facilitate spatial vision in front of the head. Resting refractive error (in anaesthetized pigeons) was mapped at different points in the visual field with streak retinoscopy and the retinal specialisation that serves the frontal field (area dorsalis) was 1.5D myopic (n=6, SE=.15D). However, at this distance (65cm), the birds were almost blind. Visual acuity thresholds measured using operant conditioning (B&W square wave gratings) with viewing restricted to the area dorsalis and the stimuli placed in steps from 5-80cm from the eye, uncovered the astonishing finding that maximum visual acuity (up to 14 cycles/degree) was sustained at only two specific distances (6.5 and 13cm) with acuity dramatically poorer at other distances. These two distances are the same two fixation distances in which the head pauses during a peck. Using infrared photokeratometry in head-fixed birds which were trained to focus on a small light over the same distances, we found that when the

eye converges during close viewing, the corneal power change alone (up to 9D) provides much of the required power to achieve clear focus. Furthermore, like the acuity-distance function, the corneal power-distance function is also saccadic-like and peaks at these same favoured distances. Thus, in the peripheral field in front of the head, a lateral-eyed granivorous bird is tuned to use an efficient system of two set focal planes and only at these preferred positions is blur minimised. The mechanism involves making use of the natural power gradient of the cornea combined with a saccadic eye vergence system

SOCIAL AND SEXUAL BEHAVIOR OF ORANGUTANS DURING PAIR FORMATION *Varvara Meshik, Moscow Zoo*

The formation of 10 pairs of orangs was observed in the Moscow Zoo from 1980-1988. On the basis of observational data, a mechanism for modifing behavioral strategies of each partner to get behavioral adjustment of partners is suggested. The dynamics of the partners' social and sexual behavior was analyzed. Every pair was observed 2-3 years after formation, and the breeding success of each pair analyzed in comparison with behavioral strategies of different partners. The role of first mating and sexual behavior in the process of behavioral adjustment of male and female orangs, in general, is discussed. Causes of partners' behavioral incompatibility are analyzed and a method of making changes in the social behavior of partner is proposed.

SPECTATING AND SPECTATORS *Robert M. Murphey, University of California, Davis*

Spectating appears to be universal among humans. Collectively, we expend immense amounts of time and resources in order to experience objects and events that are ostensibly trivial. The specific objects and events that elicit spectating, as well as the ways in which spectating is exhibited, may differ markedly among societies and individuals. Within a society, there may be strict norms of behavior and dress that are specific to particular kinds and contexts of spectating. The ubiquitous intensity of spectating behavior raises a number of questions regarding its possible phylogenetic origins, ontogeny in individuals, neurophysiological correlates, and adaptive functions. Resolution of these issues requires careful definitions of spectating and related phenomena (such as novelty-seeking and "morbid" curiosity) together with distinctions between spectators and the objects of spectating (such as athletes and entertainers) with regard to motives and benefits.

COMPARATIVE ANALYSIS OF AUDITORY LOCATION DISCRIMINATION IN RAT AND HUMAN WITH HISTORIES OF STATUS EPILEPTICUS *John C. Neill, Children's Hospital and Harvard Medical School*

LD (auditory location discrimination) was assessed in epileptic mentally retarded humans and in rat following status epilepticus. Rats were injected with saline on P (postnatal day) 20, or pilocarpine on P20 or P45, to induce status epilepticus. Rats began training on P105. Control rats acquired both discriminations immediately. Status epilepticus on P45 produced epilepsy, CA3 cell loss, and profound impairment in ALD. Status epilepticus on P20 did not cause epilepsy or hippocampal lesions; however, acquisition of the ALD was slow and erratic. Humans acquired the auditory location discrimination more rapidly than pilocarpine rat, but slower than normal rat, and had paroxysmal impairments associated with epileptiform discharge. The method, developed in normal rat, demonstrated impairment in ALD in rat and human with history of status epilepticus.

ROLE OF REINFORCEMENT IN THE SPACED-TRIAL INSTRUMENTAL PERFORMANCE OF PIGEONS (*COLUMBIA LIVIA*) *Mauricio R. Papini, Texas Christian University*

Most of our knowledge of learning processes in pigeons comes from studies in which exposure to stimuli and opportunities to respond are provided in a highly massed fashion (e.g., free-operant procedures and multiple discrete trials per session). In these situations, it is often difficult to separate the contribution of anticipatory processes from the contribution of the aftereffects of prior events to the control of current instrumental performance. In a series of experiments involving key-pecking and a single trial per day, pigeons were trained with different magnitudes of reinforcement administered either under continuous or partial reinforcement schedules. Under these conditions, the behavior of a pigeon in any single trial is assumed to be under the control of associatively reinstated memories; little or no influence is expected from events occurring during the previous trial given the 24-hr interval. Some groups were subsequently shifted to extinction while others were shifted from a large to a small magnitude of reinforcement. While acquisition performance was generally not affected by magnitude and schedule of reinforcement, extinction performance was uniformly poorer after training with small magnitudes than after training with large magnitudes. A shift from a large to a small magnitude provided no evidence of negative contrast. Finally, partial reinforcement did not lead to increased resistance to extinction. The performance of pigeons in this spaced-trial,

key-pecking situation resembles more that of fish, amphibians, and turtles trained under analogous conditions, than that of mammals. The pigeon's key-pecking response appears to be modulated by reinstated reward expectancies, but not by anticipatory frustrative reactions to the unexpected omission or reduction of reward magnitude in prior trials.

EARLY EXPERIENCE AND BEHAVIOURAL DEVELOPMENT FROM A COMPARATIVE PERSPECTIVE *Lesley J. Rogers, University of New England (Presidential Address)*

The forms of early experience that influence the development of behaviour and shape the behavioural profile (or 'personality') of the adult will be considered from a comparative perspective. The paper will present aspects of my research on the development of chicks and marmosets along with a broader perspective of research on other species. It will include discussion of the development of behavioural lateralization and mother-infant interactions that may determine both individual and gender differences in adult behaviour.

NUMERICAL COGNITION IN MONKEYS (*M. MULATTA* AND *M. ARCTOIDES*) AND CHILDREN *Yanjie Su, Peking University*

Five monkeys (two arctoides and three rhesus monkeys) and 10 children (4-4.5 years old) were trained on delayed matching-to-sample tasks to match the numerousness of units --forms with different sizes and shapes in various patterns. There were two units of difference between the matching stimulus and the nonmatching one. Four monkeys (two from of each species) and all the children completed the whole procedures. The response time (RT) after subjects reached criterion was significantly shorter than before criterion, but there was no significant difference with respect to number. When subjects had mismatchings, most combinations of sample, and two comparative stimuli, involved line pattern of the units These findings suggest that monkeys' and most children's (8/10) basic processing of number was neither counting nor unitary subitizing, but a primary prototype matching, of which the representation of number probably was a typical example. The relationship between numerical cognition and language is also discussed.

THE TEACHING OF COMPARATIVE PSYCHOLOGY IN CHINA *Yanjie Su, Peking University*

It has been more than 70 years since Prof. Zing-Yang Kuo introduced comparative psychology (CP) to China. However, it is embarrassing to report that CP in China now is taught only at Peking University. This paper discusses several key points to improve and

develop the teaching of CP in China. First, CP deserves a place in the undergraduate curriculum because of its comprehensive perspectives on behavior unmatched elsewhere. Second, textbooks that organized on the basis of the evolution, development, control and consequences of behavior are needed. It is also important to deal properly with the differences and connections among the disciplines of CP, animal behavior and sociobiology. Third, it would be helpful to develop programs where students could conduct experiments in the lab or observations in zoos and animal breeding centers as part of their course. Fourth, teaching would be improved through the integration of our own researches, and by communicating with other colleagues both in China and abroad. In addition, the relationship of the development of CP and other psychological fields in China is mentioned.

COMPARATIVE COGNITION: HUMAN NUMEROUSNESS JUDGMENTS *Roger K. Thomas, Julia A. Phillips, & Cheryl D. Young, University of Georgia*

Squirrel monkeys accurately discriminated 7 versus 8 entities (hereafter the form 7:8 will be used) whether they were "dots" (Thomas, Fowlkes & Vickery, American Journal of Psychology, 1980) or sides of randomly constructed polygons (Terrell & Thomas, Journal of Comparative Psychology, 1990). We concluded that they did not count, because they were not trained to count, and a prototype matching interpretation was proposed that was based on the assumption that the monkeys could learn to recognize manifestations of "sevenness" etc. The present study used comparable discriminanda to assess whether human subjects (college student volunteers) can make comparable judgments under conditions intended to preclude counting (200 msec stimulus presentations followed by masking stimuli). Despite limited training and testing, 17 of 20 subjects met criterion on 6:7, and 8 of 20 subjects met criterion on 7:8 in the "dots" experiment (among lower and higher numbers tested). Supporting a noncounting process, mean response times regardless of numbers of entities (ranging from 3:4 to 10:11) fell within a 0.3 sec range (0.72 - 1.01 secs) with an overall approximate mean of 0.84 sec.

SOME JAVA SPARROWS LIKE BACH RATHER THAN SCHOENBERG *Shigeru Watanabe & Mariko Nemoto, Keio University*

Four Java sparrows were tested for their musical preference. Staying at one perch produced piano music by Bach, while staying at another perch produced piano music by Schoenberg. Two of the birds showed a preference for Bach. Furthermore, these birds preferred

Vivaldi rather than E. Carter. These results suggest a consistent musical preference in the Java sparrow.

VIIIth BIENNIAL MEETING OF THE INTERNATIONAL SOCIETY FOR COMPARATIVE PSYCHOLOGY

Monteal, Canada, August 14-16th, 1996

ABSTRACTS OF POSTERS

CONTACT CALL INTERACTIONS IN ZEBRA FINCHES (TAENIOPYGIA GUTTATA) *Charles Blaich, Keith Steury, Arjun Guha, Kevin Mahoney & Pat Pettengill, Wabash College*

Previous research from our laboratory indicates that pair-bonded male and female zebra finches can use a variety of calls to initiate and maintain contact. The purpose of the present study is to determine whether contact call interactions among pair-bonded male and female zebra finches are qualitatively different from those among unpaired zebra finches. We recorded contact call interactions from paired and unpaired birds, and compared the percentage participation, percentage alternation, the number of male and female calls, the intercall duration, and intercall interval type. We found that contact call interactions among paired and unpaired zebra finches differed substantially. In addition, we also found that contact call interactions among paired zebra finches resembled song and call duets that occur in other avian species.

RAT'S BEHAVIORAL REPERTOIRE CHANGES UNDER CONDITIONAL DISCRIMINATION PROCEDURES USING DIFFERENT STIMULUS DURATIONS: ACQUISITION *Jose Lino O. Bueno & Alexandre Wagatsuma, University of Sao Paulo, Ribeirao Preto*

Rats received feature-positive discrimination (FPD) training with the following trials: (a) house light 15-sec, empty interval 5-sec, tone 5-sec and delivery of a drop of water; (b) tone 5-sec and no water. The rats were also exposed to a feature negative discrimination (FND) procedure with the trials: (c) house light 5-sec, empty interval 5-sec, noise 15-sec and no water; (d) noise 15-sec and delivery of water. The results

showed acquisition of the conditional discrimination: the frequencies of magazine-oriented behavior during the target stimuli were higher for the (P)T+ than T- and lower for (P)N- than N+. The frequencies of exploratory behaviors - rearing and sniffing far from the magazine - were higher during the feature stimuli than during the target ones. For the FND condition, the frequencies of exploratory behavior were higher during the target stimulus (P)N- than N+. The acquisition data are discussed in terms of behavioral plasticity under the temporal control of stimuli in conditional discrimination procedures.

INVISIBLE DISPLACEMENTS IN DOGS (CANIS FAMILIARIS)
Claude Dumas & Christine Brunet, Universite du Quebec a Montreal and Sylvain Gagnon, Universite du Quebec a Trois Rivieres

Research suggests that birds, mammals, and nonhuman primates possess to some degre the Piagetian concept of object permanence. However, there is still controversy regarding whether animals have the Stage ability required to master invisible displacements. The data suggest that dogs and great apes possess such abilities but birds, cats, and monkeys do not. However, the data for dogs are contradictory. Whereas, Gagnon and Dore (1992) concluded that dogs mastered invisible displacements, a recent study by Dore et al. (in press) reached the opposite conclusion. But Dore et al (in press) used a transposition task which markedly differs from the typical Piagetian task. The present research aimed at verifying the upper limit reached by dogs in object permanence. Five adult dogs (Canis familiaris) were administered both logical invisible displacements in which the experimenter showed whether the container was empty or not after each displacement, and comprehensive displacements in which the container was shown to be empty only at the end of the manipulation. The results revealed that dogs recovered the object on 55% (chance level = 50%) of the logical displacements, and on 60% of the comprehensive displacements. So these resullts suggest that dogs do not spontaneously master invisible displacements.

FOOTEDNESS IN 13 NEW ZEALAND PARAKEETS *(CYANORAMPHUS AURICEPS)*
Mildred Funk, Roosevelt University

Thirteen New Zealand parakeets (*Cyanoramphus auriceps*) were assessed for foot preferences in feeding behaviors. Nine (4 females and 5 males) were right footed, two (1 female and 1 male) were left footed. Two others used both feet equally when feeding. Other parakeets (budgerigars) have not shown "footedness" as a population or as individuals (Rogers & Workman, 1993), but they do not apparently use

their feet for any feeding behaviors as the New Zealand parakeets do. The Australian genus Platycercus, related to Cyanoramphus, has also shown a population bias to right footedness (Cannon, 1983; Rogers, 1989).

EFFECT OF APOMORPHINE AND OF AMPHETAMINE ON ACTIVITY IN GOLDFISH (*CARASSIUS AURATUS*) *V.L. Grant & B.T. Lett, Memorial University of Newfoundland*

Apomorphine and amphetamine, which increase activity in mammals, were assessed for effects in goldfish. In individual tanks, fish were observed for 5-15 min following an intraperitoneal injection of apomorphine (0.5 mg/kg), amphetamine (5.0 mg/kg), or saline. Compared to saline, apomorphine and amphetamine reduced the total time the goldfish were active (as opposed to resting on the tank floor). Although reduced activity is opposite to findings in mammals, the effect in fish, as in mammals, appears to be mediated by dopamine. Depending on dose, activity following apomorphine (2.0 mg/kg) was increased by pretreatment with a dopamine antagonist (pimozide, 0.5 mg/kg).

E. C. TOLMAN'S SCHEMATIC SOWBUG: A MECHANISTIC MODEL OF HUMAN AND ANIMAL PERFORMANCE *Nancy K. Innis, University of Western Ontario*

In the late 1930s, Edward Tolman introduced a mechanistic model of the f_3 function of his theoretical system. The model, known as the "*schematic sowbug,*" was influenced by Lewin's (1935) field theory and vector mathematics, and by Spence's (1937) idea of a generalization gradient. It was successful in predicting vicarious-trial-and-error performance under a number of different conditions. Although research in Tolman's laboratory was directed to problems suggested by the model for several years, it never caught on. This may be because the model was ahead of its time. However, it may simply be that the model's absurd label prevented people from taking it seriously.

A COMPARATIVE ANALYSIS OF SAME-DIFFERENT DISCRIMINATIONS *Jeffrey S. Katz, Robert G. Cook, & Brian R. Cavoto, Tufts University*

Do primates and avians share the ability to perform same-different visual discriminations? To explore this question pigeons were trained in a two-alternative choice task to discriminate different and same displays of four types: Texture and Feature (small colored shape elements), Geometric (large colored shape elements), and Object (birds, flowers). All types were learned at the same rate and successful transfer to novel

exemplars occurred, suggesting a single same-different rule was used with all types. A comparative analysis of concept learning is discussed.

STIMULUS-STIMULUS AND RESPONSE-STIMULUS LEARNING IN BUDGERIGARS (*MELOPSITTACUS UNDULATUS*) *Takashi Kawashima & Kazuchika Manabe, Nihon University & University of Maryland*

Budgerigars were trained both in 0-sec or 5-sec delayed color and shape identity Matching-to-Sample (MTS) tasks. The birds could get food if they chose the same comparison stimulus as the sample after making the correct differential response to the sample. In a test, color comparison stimuli were exchanged with shape stimuli, and vice versa. The results indicate that birds learned a sequence using the differential sample response and the comparison stimulus in the 0-sec delayed shape MTS task and in the 5-sec delayed MTS procedures. On the other hand, birds did not learn the response-stimulus sequence, but learned an identity matching from sample color to comparison color in the previous 0-sec delayed color MTS task.

DEPRIVATION OF FOOD OR WATER INCREASES EXPLORATORY BEHAVIOR IN THE ELEVATED PLUS MAZE *Silvio Morato, Universidade de Sao Paulo*

Deprivation of food or water may increase general activity. As anxiety measures obtained in the elevated plus maze may be influenced by alterations in general activity, male Wistar rats were submitted to different periods of food or water deprivation and then submitted to the elevated plus maze. Results show that the measures related to anxiety in this test (frequency of entries and time spent in the open arms) were decreased after 48-h deprivation of food or water, but not after 12 or 24 h. It is not clear whether deprivation has anxiolytic effects or is a contaminant in this test.

AMOUNT OF REINFORCEMENT AND INSTRUMENTAL PERFORMANCE IN TOADS (*BUFO ARENARUM*) *Ruben N. Muzio & Enrique T. Segura, University of Buenos Aires & Institute of Experimental Biology and Medicine and Mauricio R. Papini, Texas Christian University*

Previous research in a water-reinforced instrumental training situation with toads (Bufo arenarum) has shown that performance in both acquisition and extinction is poorer in animals receiving partial reinforcement training and relatively smaller magnitudes of reinforcement. Although the results can be accounted for by a simple

strengthening-weakening model, the contribution of reinforced (R) and nonreinforced (N) trials to response strength has been confounded with other factors in previous experiments. These issues were studied in a spaced-trial experiment in which 3 groups received 24 R trials (C/24), 12 R trials (C/12), or 12 R and 12 N trials in a random partial reinforcement schedule (P/24). In acquisition, terminal performance was better in C/24 than in P/24, and P/24 and C/12 showed similar terminal levels. This pattern suggests that the strengthening effect of R trials on acquisition performance is relatively stronger than the weakening effect of N trials. Nonreinforcement does result in a weakening of performance as manifested in higher latencies after N trials than after R trials in P/24--a reward-following effect. In extinction, however, the continuously reinforced groups showed lower latencies than the P/24 animals, but did not differ from each other. Extinction does not discriminate between 12 or 24 R trials, but it does discriminate between continuous and partial reinforcement schedules. No evidence was found of a partial reinforcement extinction effect or of an overtraining extinction effect, both thought to depend on an emotional reaction to the unexpected omission of reinforcement.

US POSTEXPOSURE EFFECT ON CONDITIONED FLAVOR PREFERENCE IN THE RAT *Sadahiko Nakajima and Nobuyuki Kawai, University of Pennsylvania & Kwansei Gakiun University*

Postexposure to a sucrose solution after flavor-sucrose pairings in solution attenuated conditioned flavor preference. Tthe effect depended upon the concentration of sucrose used in the postexposure. The higher the concentration, the larger the effect. An account of the postexposure effect based on erasure of incubation was rejected because of no incubation in our setting.

DISCRIMINATION OF JOHANSSON'S STIMULI IN PIGEONS *Emi Omori and Shigeru Watanabe, Keio University*

Pigeons were trained to discriminate between motions of three dots pasted on a pigeon and those pasted on a toy dog. The subjects could learn the discrimination of such Johansson's stimuli. Then they received a generalization test with motions of the real bird and the real toy dog. The subjects showed individual differences in the tests, however, some of them showed generalization to the new stimuli and transfer from the dot motion to the real movement.

MAGIC MIRROR BOXES AND SOCIAL RECOGNITION: CAN FEMALE CICHLIDS DISTINGUISH BETWEEN FAMILIAR MALES

WITHOUT SOCIAL PROMPTS? *J.R. Waas, University of Waikato*

A "two-choice" chamber was used to determine if female convict cichlids, *Cichlasoma nigrofasciatum* (N=11), could use visual cues to distinguish partners from familiar male neighbours that had similar social and physical attributes. A pair of magician's "mirror boxes," fitted with either "one-way" mirrors or "two-way" glass, were positioned at each end of the chamber to control whether the stimulus males could see and, therefore, visually interact with the tested female. The choice chamber had three equal-sized compartments that the female could move between freely. Females spent more time (c. 10-30%) in the compartment adjacent to their partner than they did in either the central "neutral" compartment or the compartment adjacent to the familiar neighbour. Females that could see and visually interact with the stimulus males during tests spent a similar amount of time with their own partners (c. 46-49%) as female that could see but not interact with the males. The results indicate that female convicts are capable of individual recognition and that they do not have to interact directly with males to discriminate between them.

MOTORIC AND SENSORY LATERAL BIASES IN THE BUSHBABY (*OTOLEMUR GARNETTII*) *C. Cantalupo, J. P. Ward, S. P. Kelley, and C. Keeney, The University of Memphis*

Twenty-seven bushbabies were videotaped while reaching for mealworms in an apparatus designed to test the animals in both quadrupedal and bipedal postures. The effects of the different motoric and perceptual rerquirements in the two postural conditions on the strength and direction of laterality in hand reaching and whole-body turning are reported. The same animals were also videotaped while viewing different stimuli (mealworms, a stuffed owl and a video camera), using an apparatus which required the animals to fixate the stimuli monocularly. The frequencies and durations of left and right monocular fixations were scored from the videotapes to assess the effects of the different stimuli on the laterality of eye use. Finally, the relationships between hand-reaching, turning, and monocular fixation are presented.

PROCESSING OF SPATIAL RELATIONS IN BABOONS (*PAPIO PAPIO*) *D. Dépy, J. Vauclair & J. Fagot, C.R.N.C., C.N.R.S.*

Distance evaluation and topological relation processing were investigated in baboons (*Papio papio*) using two video identity matching-to-sample tasks. In the distance task, monkeys were required to evaluate the distance between a horizontal line and a dot that was

located either above or below the line. In the topological task, the baboons had to decide whether the dot was above or below the line, whatever the distance separating the dot from the line. Despite the relative difficulty encountered by the baboons to simultaneously process the dot and the line, all the subjects learned both tasks. Results are discussed with respect to the processes involved in the learning of spatial relations and hemispheric specialization.

MATERNAL INVESTMENT IN SHEEP: CHANGES IN LITTER SIZE AND BIRTH SEX RATIOS *J. P. Kent, University College, Dublin*

The birth sex ratios of sheep were studied in relation to litter size, seasonal and ageing factors (Kent, 1992, 1995, 1996). However, maternal investment in sheep is not confined to variation in birth sex ratio. As sheep age the litter size increases. Further as ewes age they give birth earlier in the lambing season. Changes in the birth sex ratio are associated with changes in litter size and age of the ewe.

VARIATIONS IN THE STRUCTURE OF THE PEEP VOCALIZATION OF FEMALE DOMESTIC CHICKS (*GALLUS GALLUS DOMESTICUS*) ON DAYS FIVE AND SIX POST-HATCHING *D. J. Jennings and J. P. Kent, University College, Dublin*

Domestic chicks (*Gallus gallus domesticus*) were reared in pairs from day three post-hatching. On the fifth day of life, a chick was separated from its brood mate and 30 secs later the chicks' vocalizations were recorded for five minutes. The recordings were analysed using Canary 1.1 sound analysis system running on Mac II vx. Seven acoustic parameters of the peep vocalizations of female chicks were measured: duration (msec), maximum frequency (kHz), minimum frequency (kHz), difference between maximum and minimum frequency (kHz), peak frequency (kHz), energy (watts) and average power (joules). During separation chicks produced peep calls that differed in structure. In total, 12 female chicks' vocalizations were examined and seven chicks produced three distinct peeps . These were classified as short, medium and long. Three calls of each type for each chick were examined. Short peeps have a narrow frequency range and short duration, medium peeps have a wider frequency range, longer duration and a short upper inversion preceding the descending frequency. Long peeps have the widest frequency range, the longest duration and have the most complex structure. The main finding of this study is that the chick of the domestic fowl can produce three distinct types of peep call.

EYE-GAZE AVOIDANCE AND LEARNING IN ORANG-UTANS *Gisela Kaplan & Lesley Rogers, University of New England*

This poster focuses on eye gaze in orang-utans. In our field study of rehabilitating orang-utans we noted that attention to a stimulus and making social contact did not conform to human expectations. We have used frame-by-frame analysis and found that orang-utans persistently avoid direct frontal eye gaze both with conspecifics and with human observers. A large percentage of looking behaviour is achieved laterally with turned eyes. The lack of direct gaze does not indicate inattention because it is clear from numerous examples of research (both anecdotal and systematic) that orang-utans are extremely competent learners and imitators, solving complex tasks after a brief period of exposure and with persistent avoidance of the stimulus in question.

RAT DOMINANCE AVERSION USING UNPREDICTABLE SHOCKS AS STRESSORS *Andres P. Lemoine, Lorena Rela & Enrigue T. Segura, University of Buenos Aires & Institute of Experimental Biology and Medicine*

Pairs of naive Sprague-Dawley rats (male, adult) were randomly formed 1 month before testing. Dominance (D) was assessed by scoring priority to access to a limited water source, as well as displacement and agonistic encounters. Dominant rats were then subjected to 100 unsignaled footshocks (control dominant rats received the same number of shocks, but signaled). D was then reassessed. Results showed that unsignaled but not signaled shocks lead to a transient reversion of dominance.

EQUINE COLOUR VISION *Todd Macuda & Brian Timney, University of Western Ontario*

Equine colour vision was measured in the present study under conditions that minimized the possibility that the animals were using brightness cues to make chromatic discriminations. In a two stage study we first obtained brightness discrimination functions for achromatic targets then tested for chromatic discrimination over a range of target luminances. Horses were trained on a two choice discrimination task. The positive stimulus was varied in luminance and/or colour using neutral density and broad band colour filters (Kodak Wratten). The negative stimulus appeared as a uniform grey. In the brightness discrimination task the horses performed very well for large luminance differences but their percentage of correct responses fell to near chance levels at differences of less than .2 log units. The chromatic discrimination function for yellow matched the luminance discrimination

function, suggesting that horses cannot discriminate yellow from grey. We are currently obtaining data on a number of other spectral targets.

SUCROSE INGESTION FOR 24 H OR 14 DAYS MODIFY ANXIETY AS MEASURED IN THE ELEVATED PLUS MAZE *Silvio Morato, Universidade de Sao Paulo*

There are reports suggesting the ingestion of sucrose may decrease the frequency of behaviors that might be related to anxiety. So male Wistar rats received different sucrose solutions for 24 h or 14 days before being submitted to the elevated plus maze, a known test for experimental anxiety. After 24 h, sucrose (250 g/l) had anxiogenic effects while after 14 days (50 and 250 g/l) the effects were anxiolytic, as judged by modifications in the exploratory behavior in the open arms of the maze.

THE EFFECTS OF VARIABLE- AND FIXED-INTERVAL SCHEDULE HISTORIES ON RATES AND PATTERNING OF RESPONSE ON A FIXED-RATIO SCHEDULE *Leslie Phillmore and Mark Cole, Huron College at the University of Western Ontario*

Rats were exposed to a fixed ratio 20 schedule following exposure to either a fixed interval 30 sec schedule (two rats) or a variable interval 30 sec schedule (two rats). There was no evidence of schedule history on rate of responding on the fixed ratio schedule, but the fixed interval history led to transient post-reinforcement pausing on fixed ratio for one rat. The results support Cohen, Pederson, Kinney and Meyers (1994) in suggesting that ratio schedules are less affected by schedule histories than are interval schedules and that this is true for both patterning and rate of responding.

LATERALITY OF HAND EFFICIENCY DURING PREY CAPTURE IN THE GALAGO (*GALAGO MOHOLI*) *A. L. Rosner, J. P. Ward, D. L. Dodson, & C. F. Larson, The University of Memphis*

Direct comparisons between preferred and nonpreferred hand use in nonhuman primates is often difficult due to the relatively small number of responses made with the nonpreferred hand. The present study compared measures of reach efficiency in eight galagos (Galago moholi) tested in a reach apparatus designed to elicit equal numbers of responses by both hands. Efficiency was defined in terms of the number of successful reaches and their durations. We found that the preferred and nonpreferred hands did not differ with respect to these two measures, indicating that the apparatus was effective. However, we found that in seven of our eight subjects the left hand generated faster reach times than

did the right hand. The results are explained by a proposed species-typical right hemisphere advantage for the execution of such movements which involve quick reflexes.

PRELIMINARY EVIDENCE ABOUT HAND PREFERENCES IN WILD MURIQUIS (BRACHYTELES ARACHNOIDES) *M. Talebi-Gomes & C. Ades, University of Sao Paulo and K. B. Strier, University of Wisconsin, Madison*

Handedness in food manipulation and its relationship to posture were examined in wild muriquis (*Brachyteles arachnoides*) at the Carlos Botelho State Park, Brazil. Scan sampling records included types of food manipulation (right hand, left hand, both hands, mouth) and postures (standing, sitting, suspended by tail, lying down). Results show a significant overall right hand preference (proportion of episodes: right, 59%; left, 22%, both, 16%, mouth, 3%). Right hand preference was also clear in male and female samples as in the different age level classes. Postural context seems to influence hand preferences: animals which were suspended bythe tail exhibited less manipulation assymmetry than those in other postures. The results of this study, which will be complemented with further observations at the same and other sites of the Brazilian Atlantic forest, are relevant to hypotheses about the evolution of handedness in primates.

LLOYD MORGAN'S CANON AND THE LAW OF PARSIMONY *Roger K. Thomas, University of Georgia*

Lloyd Morgan's Canon has been generally misrepresented as being a canon of parsimony, that is, that the simplest explanation should be used. Simplicity was not Morgan's criterion. He believed that psychological processes were hierarchically organized in order of evolutionary development and that the lowest process that could explain an action should be used unless there was compelling evidence to the contrary. He viewed some higher processes as being simpler than the lower ones. The canon was also used wrongly against Romanes.

LABORATORY OPEN-FIELD AS A REDUCED SITUATION FOR STUDIES OF ANIMAL BEHAVIOUR: ITS RICHNESS *Keiichiro Tsuji, Nagoya University*

Experimental psychologists have been faced repeatedly with the criticism that laboratory works cannot lead to significant findings on adaptive behaviour, even if strict analyses might be made of the behaviours which occur in a reduced situation like the laboratory open-field. Is this criticism correct? This poster attempts to demonstrate

that it is a misconception which has prevailed among behavioural scientists. Caravaning is an early behaviour observed in many species of Crocidurinae of Insectivora. The young shrews hold onto the fur of other shrews and thus the mother moves about with a line of young trailing behind her. With the house musk shrew (*Suncus murinus*), we observed caravaning in three different situations: a laboratory open-field, an indoor living cage, and a large-sized outdoor enclosure. Caravaning in the laboratory open-field ranged from 5 to 22 days of age and had five patterns of formation in the course of development, while caravaning in the outdoor enclosure was largely limited to the range from 15 to 22 days, and showed only one of the five formation patterns. Caravaning in the living cage fell between that in these two situations. The finding suggests that the laboratory open-field can maximize the possibility for manifestation of the caravan formation patterns which are potentially built-in, but usually not disclosed. As clearly demonstrated, the behaviour patterns which occur in the laboratory open-field are more varied than those observed in the natural (quasi-natural, in this case) environment. Some of them are not adaptive for the present, but could have been significant in the evolutionary process and might be so in the future. In the area of behavioural studies, ecology and psychology could thus take reciprocal roles in that the former is concerned with the 'reality' of adaptation, while the latter with its 'potentiality'.

THE ASSOCIATION BETWEEN SCENT-MARKING, RESPONSE TO RESTRAINT STRESS, AND OVER-GROOMING IN THE SMALL-EARED BUSHBABY ((*OTOLEMUR GARNETTII*) *Sheree L. Watson, Wake Forest University and Amy Rosner & Jeannette P. Ward, The University of Memphis*

The characteristics of scent-marking behavior were examined in 21 female and 24 male bushbabies as the animals investigated a novel environment. Frequency and patterns of scent-marking were examined for sex differences. Behavioral responses to manual restraint were examined in the same bushbabies as they underwent routine veterinary examinations. To determine whether frequency of scent-marking in males was related to the individual's characteristic response to stress, the behavioral as well as cortisol responses to restraint stress were examined in males that displayed high and low levels of scent-marking. Additionally, colony medical records were examined to determine whether cortisol response to restraint stress could indentify males likely to engage in over-grooming as a self-calming mechanism.

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INDIVIDUAL DEVELOPMENT AND EVOLUTION: THE GENESIS OF NOVEL BEHAVIOR

TY PARTRIDGE
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Individual Development and Evolution: The Genesis of Novel Behavior, by Gilbert Gottlieb, Oxford University Press, N.Y., 1992, 231 pp.

Comparative psychology is concerned with the development and evolution of behavior. The discipline has received criticism, however, for both a lack of guiding theory in the aforementioned aim, and for misunderstandings of evolutionary theory. Gilbert Gottlieb's book, *Individual Development and Evolution: The Genesis of Novel Behavior*, does much to further comparative psychology's aim and answer its critics. Gottlieb's thesis is that it is ontogenetic novelty that produces evolutionary change. This is in essence an ontological reversal of mainstream evolutionary thought. In developing his argument, Gottlieb provides a conceptual framework that is significant for comparative psychology, adds to the evolutionary dialogue, and damages behavioral explanations derived from an assumption of genetic determinism.

The book is comprised of two sections. It begins with a selective historical analysis of the foundations of population genetics and embryology. Although this section is very informative and written in unusually readable prose for historical treatments, one is not sure where Gottlieb is headed at first. However, by the book's midpoint the reader is suddenly acutely aware of what Gottlieb has done. His historical treatment subtly buttresses his own theoretical argument by pointing out glaring discrepancies between explanations based on the modern-synthesis and empirical observations obtained in the area of embryology.

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Further, Gottlieb cogently demonstrates why and how such divergent paradigms as population genetics and developmental embryology became so divergent. The latter half of the book is a well articulated description of his ideas, attempting to integrate empirical knowledge of contextual effects influencing morphological and behavioral development and modern evolutionary theory. Thus, the "nature-nurture controversy" is resolved by understanding that behavior is the result not of genes, or biology, nor of nurturance, but is, rather, the result of the complex and dynamic interplay of these factors. Psychological organisms are biosocial beings, and nature and nurture are fused in their influence on behavior. One often neglected and misunderstood implication of this fusion is the bidirectionality of epigenetic processes. Genes affect an organism's phenotype, but the organism's behavior (a phenotypic characteristic) is also now shown to impact the genotype itself.

There are two important concepts in Gottlieb's approach that provide ample fuel for empirical work: those of behavioral neophenotypes and of reaction ranges. The former concept is borrowed from Z. Y. Kuo (1967) and refers to the drastic changes in behavioral development that can arise from significant alterations in the contextual conditions of usual organismic development. Gottlieb cites as an example Kuo's experiment in which the previously thought instinctive sexual behavior of male dogs was virtually reversed by controlling the experiential history of the animals. Essential to the creation of neophenotypes are the timing, duration, and quality of contextual alteration.

The second concept discussed is that of the norm of reaction, which is contrasted with the concept of the reaction-range. Largely as the result of mainstream evolutionary thinking, which takes a neo-Haeckelian approach, it has been assumed that an organism's genotype sets narrow limits on the range of phenotypic expression. This line of thinking is referred to as the reaction-range concept. In contrast, the norm of reaction concept assumes that there are no presupposed limits on phenotypic expression. In this conception, genes are limited to a necessary role but of a more limited ontogenetic significance than they have typically been granted.

These two concepts provide propositions from which enormous intraspecies behavioral plasticity can be deduced. Further, these behavioral novelties, Gottlieb contends, can be, and are canalized to produce speciation. While Gottlieb was certainly not the first to recognize or discuss this (e.g., Plotkin, 1988), that his very readable discussion includes evidence for this process should do much to assure

its broad acceptance by biologists and psychologists alike.

Comparative psychologists have been criticized for making comparisons between species that are not phylogeneticaly related. By coupling the aforementioned concepts with the concept of integrative levels, Gottlieb not only refocuses the discipline of comparative psychology but effectively silences it's critics. In short the argument is as follows; differential behavioral phenotypes are primarily the result of supragenetic influences. The impact of these influences is dependent upon temporal factors. Further, the malleability of any given species is dependent upon the complexity and integration of the organism. Thus, comparisons regarding the degree of ontogenetic plasticity, "causes" of that plasticity, and rates of evolution and adaptability can be made not on a clade basis but a grade basis. This orientation provides plenty of work for comparative psychology and addresses the criticism that the levels concept is not a heuristic for us.

The anagenetic model discussed by Gottlieb here and in earlier pieces was developed by Schneirla into an hierachical or integrative-levels understanding of behavioral evolution. One of the main concepts of the levels notion is that as one moves up the levels, an increase in behavioral plasticity is apparent. The higher levels include more complex and varied behaviors. From a reductionist perspective, and looking only at genes in evolution, it is true that the levels concept is not of much help. However, from the epiegenetic perspective taken by Gottlieb, with its shift from genes to a holistic approach, shows the levels concept to be both intuitive and vitally important. Based on the work of Jerrison, Razran and others, Gottlieb points out that increased behavioral plasticity occurs in animals with higher brain to body ratios. The more behaviorally plastic a species is, the more likely it is to develop latent morphological changes when faced with change and the more likely an animal is to be affected by experiences the more likely it is that morphologcal change will result from those experiences. Species that are more plastic are better equipped to adapt to change. Gottlieb's contention that different adaptive demands on an organism bring out latent morphological changes that then allow a genetically based evolutionary change to follow, is a powerful one. The levels concept, in this light, is central to the concept of evolution - for both its predictive power, and its theoretical base.

As many important works do, this book has implications beyond a single discipline. As such, Gottlieb's ideas have significant contributions to make to the related fields of evolutionary biology and population genetics, although, the contribution is more positive for the former. While at first glance Gottlieb's argument seems to be

antithetical to the modern synthesis, in fact the two, are not incompatible. To incorporate Gottlieb's thesis, modern evolutionary thought need only to rethink the rate of speciation and the mechanism of variation. Rate of speciation is already under considerable discussion within the field of evolutionary biology as the result of the punctuated equilibrium theory promulgated by Eldridge and Gould (1972). Indeed, Gottlieb's thesis, in concert with natural selection, may provide a potential mechanism by which punctuated equilibrium occurs. Additionally, Gottlieb's discussion of the findings of developmental embryology challenges the Mendelian concepts of population genetics.

It is not uncommon in science to find little more than lip service granted to important concepts. In 12 years and six biennial T. C. Schneirla conferences organized around the concept of "integrative levels" (Greenberg & Tobach, 1984) we have found that while most scientists acknowledge the significance of this crucial organizing principle, reductionistic thinking still prevails in the behavioral and the biological sciences. With respect to the book under review here, the same can be said of the concept of development and its significance for understanding evolution and evolutionary theory (on this point see too, Michel & Moore, 1995). Gottlieb's is an important book for all evolutionary scientists, not least because, in his own words: "It is now acknowledged in many different quarters, both within and without the modern synthesis...., that the time has come to include the role of individual development in evolution and I cannot but hope that this small book makes some contribution toward that aim" (p. 194). In accomplishing this goal Gottlieb takes us through more than 200 years of thinking about development, embryology, and evolution to illustrate and underscore the dramatic importance of development in the evolutionary process.

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